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DOI: https://doi.org/10.1007/s00442-005-0341-8

Oecologia (2006) 148: 144–152
DOI 10.1007/s00442-005-0341-8

CONSERVATION ECOLOGY

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Received: 26 May 2005 / Accepted: 14 December 2005 / Published online: 21 January 2006

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Keywords Extinction · Fragment size · Generalists/specialists · Interaction stochasticity · Species turnover

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00442-005-0341-8 and is accessible for authorized users.

Communicated by Christian Koerner

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Introduction

One of the most dramatic landscape changes during the twentieth century in Europe has been the reduction and fragmentation of habitats such as semi-natural grasslands (Fischer and Stöcklin 1997; Eriksson and Ehrlén 2001; Kiviniemi and Eriksson 2002; WallisDeVries et al. 2002). Habitat fragmentation, the transformation of once large and continuous habitat areas into a number of small and isolated patches, is nowadays one of the most important threats to local biodiversity (Groom and Schumaker 1993), and the interaction of habitat fragmentation and rapid climate change is predicted to lead to a range-wide increase in extinction risk (Jump and Penuelas 2005). Habitat fragmentation reduces the area available for species and leads to isolation and decreased size of remnant populations in plants and animals, which may suffer from increased risk of local extinctions (Gilpin and Soulé 1986; Saccheri et al. 1998). The disadvantages suffered by small populations involve greater sensitivity to demographic stochasticity (Holsinger 2000) and reduced genetic variation (Ellstrand and Elam 1993; Lynch et al. 1995; Fischer and Matthies 1997; Krauss et al. 2004). Furthermore, effects of habitat fragmentation on individual species or populations may lead to the disruption of biotic interactions such as pollination or seed dispersal (Lennartsson 2002) and hence can affect species with previously stable populations. These different processes may occur together and reinforce each other leading to an extinction vortex (Shaffer 1981; Menges 1991).

In plants, the fate of remnant populations within habitat patches or land-bridge islands (Forman 1995)

will depend on the degree of isolation, the quality of the matrix habitat, the size of the remnant population, and on species characteristics such as mating system, seed dispersal ability, seed dormancy, and plant longevity (Charlesworth and Charlesworth 1987; Kareiva 1987; Saunders et al. 1991; Fischer and Matthies 1997; Stöcklin and Fischer 1999; Aizen et al. 2002; Soons and Heil 2002). In addition, altered abiotic conditions associated with edge effects due to fragmentation have also been found to influence species dynamics in several experimental studies (Bruna 1999; Debinski and Holt 2000; Laurance et al. 2002; Dolt et al. 2005). All these factors may lead to increased extinction rates in habitat islands, particularly if they are of small size.

Due to isolation, the colonization by new species or the re-colonization by previously present species is expected to be lower in fragments than in sections of continuous habitat of the same area (MacArthur and Wilson 1963; Levins 1970; Hanski 1991a, b; Gonzalez et al. 1998). Changed extinction and colonization rates in fragments may subsequently lead to shifts in community composition (Robinson et al. 1992) and result in a net decline of species richness. However, very few studies have tested the causes of temporal changes in community structure (Manne et al. 1998) and such shifts have rarely been empirically investigated in fragmentation studies (Debinski and Holt 2000). Only a few fragmentation experiments with proper replication and controls have been carried out (Debinski and Holt 2000) and, in contrast to expectations, often showed transitory increases in species richness in fragments, due to invading generalists from the surrounding matrix and due to a competitive release of suppressed species because of edge effects (Holt et al. 1995, Debinski and Holt 2000).

Here, we report results from a 7-year habitat fragmentation experiment in natural mesocosms (Srivastava et al. 2004) with a treatment-versus-control design to address predictions made by biogeographic (MacArthur and Wilson 1963), metapopulation and metacommunity (Hanski 1999; Leibold et al. 2004) theories. Our open, natural mesocosms allowed for replicated communities of different size classes and allowed for the comparison of community changes in fragments with community changes in adjacent non-isolated control areas of the same sizes. By frequent mowing of the surrounding area, we fragmented species-rich calcareous grasslands spread over three sites in the Swiss Jura Mountains in 12 experimental blocks containing 48 small fragment plots, separated by 5 m from each other and from the adjacent continuous habitat. In the adjacent continuous habitat, 48 control plots of the same size as the fragment plots were marked. Calcareous, nutrient-poor grasslands are ideal model ecosystems as they allow experimental fragmentation at a scale that is large relative to the size of the plant species typically found in this type of vegetation. During 7 years, we followed the vegetation dynamics within fragments and control patches to quantify extinction and colonization rates and their net effects on plant community composition and species richness. We tested the following two hypotheses: (1) fragmentation leads to decreased colonization rates compared with control areas and, together with (2), to reduced species richness in habitat remnants; and (2) extinction rate increases with decreasing patch size both in fragment and control plots, but the effect is stronger in fragments.

Materials and methods

Field sites and experimental design

Our model ecosystems were nutrient-poor, dry, calcareous grasslands characterized by the presence of the grass *Bromus erectus* (*Mesobromion*-alliance, Ellenberg 1988). This vegetation harbors a large number of dwarf flowering plants at the square-meter scale (Zoller 1954) and is thus particularly suited for experimental tests of habitat fragmentation using relatively small patches of land that allow adequate replication at the landscape scale. We established a total of 12 blocks for the application of fragmentation treatments at three field sites in the Swiss Jura Mountains: ''Nenzlingen'' (47°28′N, 7°34′E, 510 m asl), ''Vicques'' (47°22′N, 7°26′E, 590 m asl) and ''Movelier'' (47°25′N, 7°20′E, 770 m asl). These three sites were located within 20 km of each other and were also used to study various other groups of organisms (Baur et al. 1996; Zschokke et al. 2000; Groppe et al. 2001; Goverde et al. 2002). Until the start of the experiment, the study sites were used as cattle pastures at a relatively low stocking rate. During the experiment, this use was replaced by yearly mowing in late autumn. Therefore, appropriate controls were of particular importance.

The 12 blocks measuring 32×29 m each were set up in April 1993 (according to size of field sites, five blocks could be placed in Nenzlingen, four in Vicques and three in Movelier). Each block was divided into two halves of 32×14.5 m. In each half of a block, four quadratic patches of vegetation (plots of geometrically increasing area: 0.25 m^2 < 2.25 m^2 < 20.25 m^2) were established (see Fig. 1). The smallest plot size occurred twice in each half of a block, because we anticipated larger variation in species composition among small plots. The positions of control and treatment halves and of plots of a given size within halves were randomly allocated in each of the 12 blocks. At the beginning of the experiment, plots of 0.25 m^2 on average harbored 23.3 plant species (including woody species), plots of 2.25 m^2 43.0 plant species and plots of 20.25 m^2 65.3 plant species.

In the treatment halves, fragmentation was imposed by frequent mowing (6–12 times between March and October) of the interstitial matrix vegetation leading to an isolation distance of 5 m both between plots and between plots and continuous vegetation. Mowing prevented any seed-set of species surviving in the matrix vegetation. In particular, dwarf shrubs such as *Helianthemum nummularium*, *Genista sagittalis*, *Euphorbia*

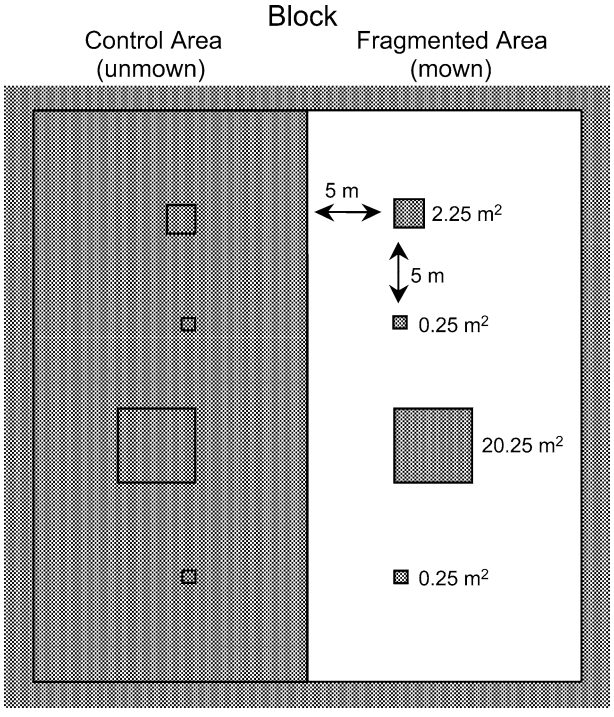

Fig. 1 Layout of one of the 12 blocks that were set up in the field in early spring 1993. Each block contained four small plots of 0.5×0.5 m, two medium-sized plots of 1.5×1.5 m and two large plots of 4.5×4.5 m. Half of each block served as control, the other half was experimentally fragmented by frequent mowing between plots. Isolation distance between fragment plots and these and continuous vegetation was 5 m. The position of each pair of plots of a given size as well as the position of control and treatment side was randomly chosen in each of the 12 blocks

cyparissias and *Ononis repens*—here and in the following, taxonomy always follows Lauber and Wagner (1996)—declined in the matrix vegetation, whereas sun-loving herbs such as *Hieracium pilosella*, *Prunella grandiflora*, *Prunella vulgaris*, *Bromus erectus*, *Thymus serpyllum*, and *Sedum sexangulare* (the six most common species in the matrix) persisted in the matrix vegetation. No mowing between plots was applied in the control halves. Therefore, these controls represented sample plots in the continuous vegetation (Fig. 1). At the end of the season each year, the entire experimental area was mown to simulate the previous grazing regime and prevent succession (Zschokke et al. 2000).

Vegetation survey and data preparation

Starting in 1993, plant species richness was recorded annually (with the exception of 1998 where no data were collected) in spring and summer (beginning of May, July/August) at the level of individual plots, using portable scaffolds to prevent trampling of the plots. Initial plant-species lists recorded in 1993 are presented in Baur et al. (1996). In the first year, vegetation was sampled with greater detail than in the subsequent years because the first-year data served as the baseline for future extinction and colonization events. In 1993, rooting shoots and rosettes of herbaceous plants and culms of grasses and graminoids were counted in each plot. To calculate initial average population sizes on a per plot base, graminoids and woody plants were excluded and the average number of rooting shoots and rosettes of a total of 76 herbaceous species was used. The Shannon diversity index (H'), the Simpson index (D), and an evenness index (Hill's modified ratio E5; Ludwig and Reynolds 1988) were calculated from these abundance data. Shannon's diversity index was calculated as $H' = -\Sigma p_i \ln(p_i)$, where p_i denotes the proportional abundance of the i-th species. In a sample with only one species, H' becomes 0. The Simpson Index (D) was estimated as $D = \Sigma p_i^2$. The Simpson Index gives the probability that two individuals drawn at random from a community belong to the same species. Hill's modified ratio (E5) was calculated as $E5 = (1/D) - 1/e^{H'} - 1$ (Ludwig and Reynolds 1988). If all species in a community are equally abundant, i.e. evenness is maximal, E5 becomes 1. Otherwise, if only one species dominates the community E5 equals 0. To assess how well the pattern of species abundance followed a log-normal distribution, Pielou's (1975) method of fitting a truncated log normal curve was used.

During the 7 years, vegetation surveys were carried out by three different botanists (1993–95 by J.J., 1996 and 1999 by H.-P.R., and 1997 by C.D.). The change in observer between 1995 and 1996 coincided with an unusually dry start of the vegetation period in the Jura Mountains in 1996. As vegetation surveys were not carried out in the whole area of the medium and large plots in 1997, these data were omitted from most analyses. They were, however, used to check for re-appearance of species present in 1993 and not thereafter (see below). For the calculation of extinction and colonization rates and of species turnover between 1993 and 1999, woody species were excluded, as these were annually removed by the mowing management. Species turnover rates (TR) were calculated based on presence/absence data as $TR = 100(E + C)/(S_1 + S_2)$. C is the number of colonizing species and E the number of species going extinct between censuses, S_1 the number of species present at census date 1 (1993 or 1996, respectively) and S_2 the number of species present at census date 2 (1995 or 1999), all on a per-plot basis. Extinction (ER) and colonization rates (CR) were calculated as $ER = 100(E/0.5)/(S_1 + S_2)$ and $CR = 100(C/0.5)/(S_1 + S_2)$, respectively (Nilsson and Nilsson 1982). To reduce the amount of pseudo-turnover, i.e. sampling errors that artificially increase species turnover estimates especially when comparing turnover at different plot sizes (see Nilsson and Nilsson 1985), species were only considered extinct if they were recorded in 1993 (or 1996 for analyses on species turnover during the second half of the experiment), but not in any subsequent year. On the other hand, species were counted as colonizers if they were not present before census date 2 within one of the two census periods.

Habitat specificity values 0 (none), 1 (medium), and 2 (high) were assigned to species by counting the number of phytosociological orders in which they occur in Switzerland according to the literature (see Fischer and Stöcklin 1997 for a detailed description for the habitat specificity scoring; electronic supplementary material). Each plot was also characterized by the mean nutrient indicator value of species present (nutrient indicator values of Landolt 1977). Nutrient indicator values range from 1 (plants growing on nutrient poor soils only) to 5 (plants growing on over-fertilized soils).

Statistical analyses

According to the hierarchical experimental design, the data were analyzed with analysis of variance and deviance using generalized linear modeling (McCullagh and Nelder 1989) as implemented in the Genstat 5 statistical language (General Statistical Program, release 3.2; Payne et al. 1993). The treatment model consisted of site, fragmentation, and plot-size effects (the latter partitioned into linear contrast and deviation) and their interactions (Table 1; see also Groppe et al. 2001). The block effects were fitted to eliminate spatial variation within experimental sites and site effects were tested against the variation between blocks within sites. The effects of fragmentation were tested against the variation between halves within blocks (Fig. 1; Table 1 "block × fragmentation"). Where necessary, dependent variables were transformed prior to statistical analysis to meet the analysis of variance assumptions of homoscedasticity and normality. Differences in habitat specificity of species among plots were analyzed by analysis of deviance (Joshi et al. 2001).

Table 1 Skeleton analysis of variance for measured variables. Random effects (error model) in italic letters, fixed effects (treatment model) in roman letters; effects are always adjusted for effects that precede them

Source of variation	*df*	Mean square	Variance-ratio
Site	2	MS_s	MS_s/MS_b
Block (within site)	9	MS_b	MS_b/MS_{bp}
Fragmentation	1	MS_i	MS_i/MS_{bi}
[Site × fragmentation	2	MS_{si}	MS_{si}/MS_{bi}][a]
Block × *fragmentation*	9	MS_{bi}	MS_{bi}/MS_{bip}
[Plot-pair	3	MS_p	MS_p/MS_{bp}][a]
Plot size	2	MS_a	MS_a/MS_{bp}
Plot size, linear	1	MS_l	MS_l/MS_{bp}
Plot size, quadratic	1	MS_q	MS_q/MS_{bp}
[Site × plot-pair	6	MS_{sp}	MS_{sp}/MS_{bp}][a]
Block × *plot-pair*	27	MS_{bp}	MS_{bp}/MS_{bip}
Fragmentation × plot size	2	MS_{ia}	MS_{ia}/MS_{bip}
Fragmentation × plot size, linear	1	MS_{il}	MS_{il}/MS_{bip}
Fragmentation × plot size, quadratic	1	MS_{iq}	MS_{iq}/MS_{bip}
Block × *fragmentation* × *plot-pair*	27	MS_{bip}	MS_{bip}/MS_e
Individual	$N = 96$	MS_e	

[a]These lines were not of direct interest and only included in the model if their *F*-values were larger than 2 (see Green and Tukey 1960), otherwise they were pooled with the random effect below them

Results

Species richness and composition at the start of the experiment

At the beginning of the experiment in 1993, a total of 143 plant species (including woody species) were recorded at the three study sites with 53.8% of the species occurring at all sites. Of these 143 species, 90% were perennials. The high overall mean values of the Shannon and evenness indices and the low value of the Simpson index at the beginning of the fragmentation experiment emphasize the high diversity and evenness of the investigated calcareous grassland communities ($H' = 2.88$; $E5 = 0.68$, $D = 0.09$). No significant initial differences in the pattern of plant-species diversity between fragments and control areas or between the three sites were detected with any measure, i.e. species richness, Simpson's, Shannon's, or evenness index ($P > 0.4$ for species richness and $P > 0.1$, respectively for all diversity measures).

Changes in species richness over time

On average, species richness per plot was similar in 1993 (37.6 ± 16.7) and in 1999 (35.7 ± 15.3). At the beginning of the experiment, species richness was slightly, but not significantly higher in fragment than in control plots (38.50 ± 16.89 compared with 36.67 ± 16.37; $F_{1,11} = 2.95$, $P = 0.11$). At the end of the experiment, this difference was reversed (35.52 ± 15.91 species in fragmented plots compared with 35.83 ± 15.35 species in controls) and fragment plots had a slightly, but not significantly, higher decline in species richness than control plots ($F_{1,11} = 3.44$, $P = 0.091$, -3 species vs. -0.8 species). There were pronounced differences in richness changes due to fragmentation at the different sites at the end of the experiment ($F_{2,9} = 12.89$, $P < 0.01$). Species number decreased more in fragment than in control plots at the site Nenzlingen (9.0 species less in fragments compared with 4.1 species less in controls), increased less in fragment than in control plots at the site Movelier (2.8 species more in fragments compared with 3.9 species more in controls) and remained constant in Vicques (0.2 species more in fragments compared with 0.3 species less in controls).

Colonization–extinction dynamics

Between 1993 and 1999, colonization rate was 29.4% lower in fragment than in control plots (Table 2; Fig. 2).

Table 2 Results of ANOVA for colonization and extinction rate of fragmented and control plots between 1993 and 1999

Source of variation		Colonization rate			Extinction rate		
	df	MS	*F*	*P*	MS	*F*	*P*
Site	2	27.47	0.49	0.6268	687.12	3.92	0.060
Block	9	55.81	1.17	0.3440	175.34	7.43	0.000
Fragmentation	1	394.14	7.23	0.0211	37.15	0.52	0.486
Block × fragmentation	11	54.53	1.14	0.3601	71.44	3.03	0.006
Plot-pair	3	10.03	0.30	0.8252	72.16	1.30	0.292
Plot size, linear	1	1,054.86	31.54	0.0000	439.90	7.93	0.008
Plot size, deviation	1	273.11	8.16	0.0076	135.16	2.44	0.129
Block × plot-pair	31	33.45	0.70	0.8388	55.48	2.35	0.008
Fragmentation × plot size	2	45.62	0.96	0.3941	42.91	1.82	0.178
Residual	34	47.66			23.60		
Total	95						

The extinction rate between 1993 and 1999, however, was not significantly different between fragment and control plots (Table 2). Therefore, the lower colonization rate in fragment plots decreased the species turnover rate compared to control plots by 22% ($F_{1,11} = 7.24$, $P < 0.05$; Fig. 2).

In the first half of the experiment, from 1993 to 1995, the same pattern of change was already being observed: colonization rate was decreased by fragmentation ($F_{1,11} = 25.20$, $P < 0.001$) whereas the extinction rate was not significantly affected ($P = 0.23$). This resulted in a decreased turnover rate in fragment compared with control plots ($F_{1,11} = 19.74$, $P = 0.0016$). In the second half of the experiment, from 1996 to 1999, the colonization rate was still lower in fragment than in control plots ($F_{1,11} = 5.54$, $P < 0.05$) and, overall, the species extinction rate similar ($F_{1,11} = 2.02$, $P > 0.18$). However, because at two of the three sites the extinction rate tended to be increased by fragmentation (Fig. 3), the turnover rate was no longer significantly different ($P = 0.12$) between fragment and control plots during the second half of the experiment.

At the beginning of the experiments in 1993, the logarithm of species richness increased with the logarithm of plot size (slope of the species-area curve $z = 0.24$; $R^2 = 0.89$, $n = 96$). Average population sizes of species did not differ between sites or between fragment and control plots (all $P > 0.6$), but they linearly increased with increasing plot size ($F_{1,31} = 566.9$, $P < 0.001$; see Table 3 for average population sizes of the four most common non-clonal forbs), reflecting more or less constant population densities of 2.3 "individuals", i.e. rooting shoots or rosettes per m^2.

Plot size, independently of the fragmentation treatment, had a negative influence on species colonization rate (Table 2), i.e. the newly arriving species made up a larger proportion of species present in small than in large plots (Fig. 2). In the first half of the experiment, between 1993 and 1995, no significant effect of plot size on extinction rate was observed ($P > 0.8$). However, calculated over the entire period of the experiment (1993–1999), plot size also had a negative influence on species extinction rate (Table 2), i.e. a larger proportion of species present disappeared in small than in large plots. Therefore, species turnover was lowest in large plots (−53.8% compared with small plots), i.e. small plots had the lowest, and large plots the highest, persistence in species composition over time (Fig. 2).

Species richness at the beginning of the experiment in 1993 was positively correlated with the number of extinctions between 1993 and 1999 in the small fragmented plots (Fig. 4; $R^2 = 0.41$, $F_{1,22} = 16.83$, $P < 0.001$). Such a positive relationship was lost in the medium and large fragmented plots ($P > 0.19$ and $P > 0.9$, respectively) and was not detected in control plots of any size class.

Species-specific effects

The number of generalist plant species (habitat specificity 0) did not change during the experiment (1993–1999; $P > 0.1$). However, the number of species with habitat specificity 1, i.e. species typically found in this vegetation, significantly decreased in fragmented plots of all size classes between 1993 and 1999 (−0.7 species in small plots, −0.3 species in medium-sized plots, and −3.7 species in large plots; $F_{1,11} = 8.03$, $P = 0.016$). In control plots, however, the number of specialist species with habitat specificity 1 slightly increased during the 7 years (+1.3 species in small plots, +0.4 species in medium sized plots, and +0.3 species in large plots; $F_{1,11} = 8.03$, $P = 0.016$). Only 16.8% of all species, e.g. the rare orchid *Spiranthes spiralis* or the rare legume *Trifolium ochroleucon*, had habitat specificity 2. Their number did not significantly change between 1993 and 1999 ($P > 0.3$). Generalists tolerate a broader range of habitats, reflected in a higher average nutrient indicator value of 3.17 ± 0.01, than species with habitat specificity 1 or 2, which showed lower tolerance for nutrients (average 2.29 ± 0.08 and 2.16 ± 0.1, respectively; $F_{1,132} = 58.0$, $P < 0.001$).

The same pattern was already detectable in the first half of the experiment (1993–1995): the number of

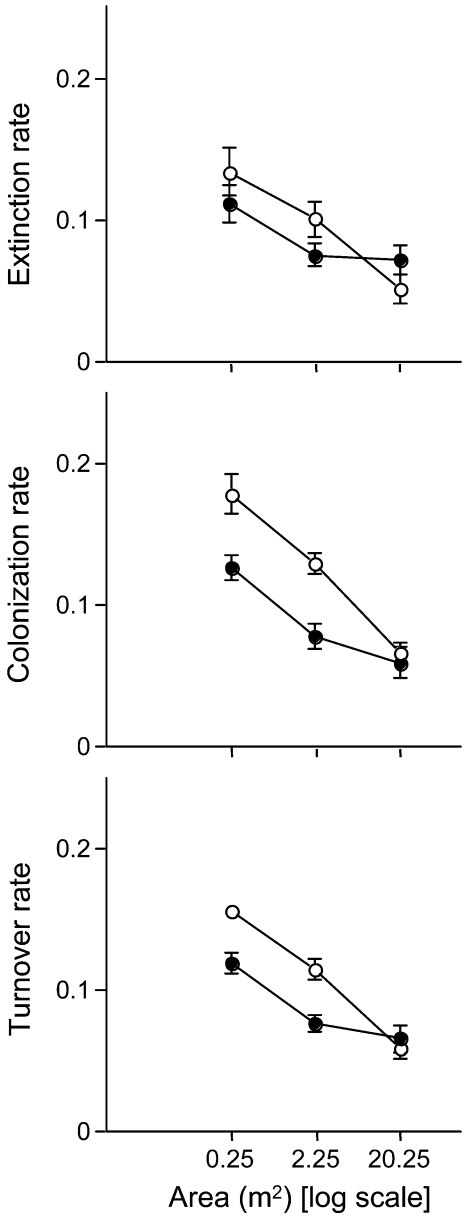

Fig. 2 Extinction rate, colonization rate, and species turnover rate, respectively, as a function of plot size in fragments (*closed circles*) and control plots (*open circles*) over 7 years, between 1993 and 1999. *Vertical bars* denote ±1 SE

generalist plant species (habitat specificity 0) and the number with habitat specificity 2 did not change during the first half of the experiment ($P > 0.9$ and $P > 0.3$). However, the number of species with habitat specificity 1 significantly decreased in fragment plots 2 years after the start of the fragmentation treatment by 8% on average ($F_{1,11} = 6.27$, $P < 0.05$).

Discussion

As predicted by the theory of island biogeography (MacArthur and Wilson 1963), habitat fragmentation

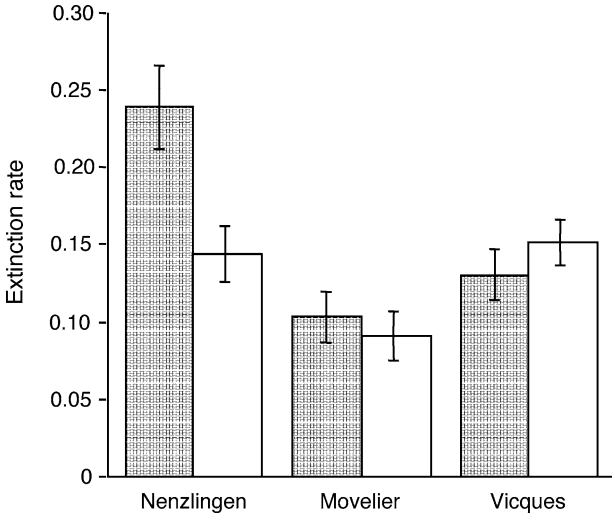

Fig. 3 Extinction rate in fragments (*filled bars*) and control plots (*open bars*) based on species present in 1993, at the start of the experiment, but not in any subsequent year until 1999, the end of the experiment, at each of the three sites. The extinction rate was highest in Nenzlingen (extinction rate in fragment plots vs control plots: 23.8 ± 2.68% vs 14.3 ± 1.83%)

had a negative impact on colonization rates of plant species in our small-scale experimental model system. The results of the present study show that even an isolation distance of 5 m reduces colonization rates. In particular, the colonization rate of habitat specialists, whose fate is of particular concern for nature conservation, was smaller in fragment than in control plots, whereas generalists were not affected by habitat fragmentation. The extinction rate of plant species during the 7-year observation period was negatively related to plot size, i.e. smaller populations had a higher chance of extinction. This is also in agreement with predictions of island biogeography (MacArthur and Wilson 1963). Hence, classical island theory is useful to study diversity patterns in terrestrial habitat remnants, albeit with some restrictions, e.g. the spillover of matrix species from the interstitial areas between fragments, which has to be taken into account (Cook et al. 2002).

Above all, initially species-rich small plots lost species due to fragmentation. In the second half of the experiment, there was a tendency of increased extinction rates in fragment as compared with control plots at two of the three field sites. Overall, the reduced colonization rate in fragment plots and the tendency of increased extinction rates in fragments in the second half of the experiment resulted in a trend of fragment plots having a higher reduction in species number than adjacent control plots after 7 years of experimental habitat fragmentation. In our study, rates were more sensitive to detect changes in community dynamics than species number per se due to random differences in initial species numbers at the different field sites between fragment and control plots. This higher variability or background noise in field experiments compared with laboratory experiments

Table 3 Average population sizes ± 1 SE in plots of different sizes of the four most frequently encountered non-clonal forbs in 1993 at the beginning of the experiment

Species	Proportion of plots containing the species (%)	Number of individuals in 0.25 m^2 plots	Number of individuals in 2.25 m^2 plots	Number of individuals in 20.25 m^2 plots
Sanguisorba minor	96.9	4.2 ± 2.9	19.6 ± 16.8	84.8 ± 29.4
Ranunculus bulbosus	88.5	6.3 ± 7.0	30.9 ± 26.6	55.8 ± 62.2
Lotus corniculatus	83.3	5.7 ± 4.7	22.8 ± 17.2	123.7 ± 72.3
Plantago media	72.9	2.0 ± 1.6	8.0 ± 9.3	39.0 ± 32.4

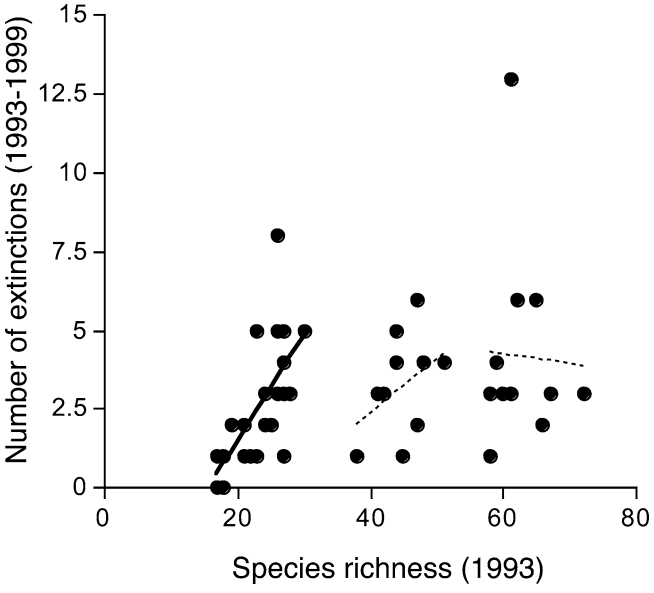

Fig. 4 Number of extinctions between 1993 and 1999 and initial species richness in fragment plots. The number of extinctions was positively correlated with species richness in small fragmented plots ($R^2 = 0.41$, $F_{1,22} = 16.83$, $P < 0.001$; *solid line*), but not in medium and large sized plots ($P > 0.19$ and $P > 0.9$, respectively; *dashed lines*)

makes it a necessity to replicate field experiments at different field sites to achieve some generality in the patterns observed.

Although our results support the theory of island biogeography, they are in contrast with an array of long-term studies, which found inconsistent effects of habitat fragmentation on community dynamics depending on ecosystem type, dispersal ability of organisms and experimental design (Debinski and Holt 2000). However, the review by Debinski and Holt (2000) showed that effects of fragmentation become stronger with time; a pattern also observed in the present study with perennial plants. Slower population growth rates in fragmented areas compared with continuous habitat increasing the risk of population decline and extinction have also been observed in an Amazonian understory herb (Bruna and Oli 2005), and higher extinction and lower colonization rates have been reported for specialist butterfly species in fragmented calcareous grasslands in Germany (Krauss et al. 2003). The low (re-)colonization rates of specialist plants in our fragment plots are matching patterns of changed plant-community composition, especially the decline of specialist plant species and the simultaneous increase of generalist plant species in habitat remnants, reported in an observational study on fragmentation effects between 1950 and 1985 at the landscape scale in the same type of grassland and geographical region (Fischer and Stöcklin 1997; Stöcklin and Fischer 1999). Plant diversity in grasslands is limited by seed dispersal and availability of micro-sites for recruitment (Tilman 1997, Turnbull et al. 2000). Our results suggest that (re-)colonization is a crucial point in fragmented habitats as control plots in continuous vegetation hold demes of plant species that are in constant exchange of individuals by seed dispersal with adjacent patches, which have been removed around the fragment plots (Holt 1992).

The low sensitivity of generalist plant species to habitat fragmentation may be due to a broad tolerance towards altered abiotic conditions as indicated by their broad range of soil nitrogen tolerance, allowing them to survive outside the habitat islands, or simply reflect their generally higher regional abundance and thus higher re-colonization pressure. Similar interpretations have been given for rain-forest fragments in the Amazon, where invasion of generalist matrix species led to an increase of generalist animal species in fragments at the expense of specialists (Laurance et al. 2002).

Plot size, independently of the fragmentation treatment, was negatively correlated with colonization rate because large plots already contained a larger number of species so that fewer new ones could be added (MacArthur and Wilson 1963). This effect, together with the decreased extinction rate with increasing plot size, also explains the lower species turnover rate in larger plots that had the highest persistence in species composition over time (see Fig. 2).

Fewer species (re-)colonized than went extinct in the surveys on species turnover over the first 3 and the last 4 years of the experiment. In the calculations over the whole duration of the experiment, this difference disappeared. This suggests that some of the extinctions observed over a short time scale were due to pseudo-extinction (Nilsson and Nilsson 1985) of species that do not produce aboveground parts in some years. The changed colonization and extinction rates did not have an immediate strong negative effect on overall species richness in fragments, but resulted in a trend of decreased species richness in habitat fragments. Especially, at the most nutrient-rich site "Nenzlingen" (Dolt et al.

2005) with the highest difference in the extinction rate between fragment and control plots, species number was less than half in fragment compared with control plots after 7 years of isolation.

In the long term, fragmentation may lead to higher extinction not only due to increased demographic and genetic stochasticity of populations, but also via indirect effects. These include altered abiotic conditions or the disruption of biological interactions (Groppe et al. 2001; Goverde et al. 2002; Braschler and Baur 2003; Braschler et al. 2003). In contrast to pure demographic and environmental stochasticity, which directly influences small populations, these combined factors that include indirect effects induced by fragmentation may be summarized by "interaction stochasticity". Stochastic interaction effects might also have influenced plant community patterns in the present study system, where fragmentation also affected species richness and density of invertebrates (Zschokke et al. 2000; Braschler and Baur 2003; Braschler et al. 2003).

While we can expect to detect shifts in species compositions due to fragmentation already after a few years (e.g. Robinson et al. 1992), the effects of habitat fragmentation on species richness may only become visible in the long run (Eriksson 1996), especially if plant communities consist of perennials that may persist for years, albeit with decreasing abundances. The lower colonization rate of habitat specialists and the trend for a higher extinction rate observed in our experimental study show that in species-rich calcareous grasslands, population dynamics can be disrupted even at the small scale of a 5-m isolation distance.

Acknowledgements We thank all the people who helped in the field during these years, Jürg Stöcklin and Markus Fischer for providing a table with specificity values of plants growing in calcareous grasslands in Switzerland, Jochen Krauss and two anonymous reviewers for helpful comments on the manuscript, and Philipp Egli for statistical advice. This project was supported by grants from the Swiss National Science Foundation (Priority Programme Environment, Module Biodiversity, No. 5001-35229 and No. 5001-044620).

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